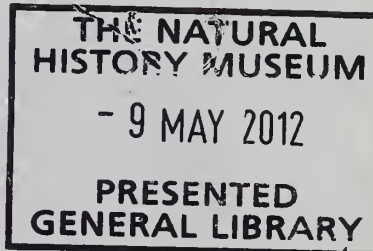


Terebratula californiana Küster, 1844, and reappraisal of west coast north American brachiopod species referred to the genus *Laqueus* Dall, 1870



D. I. MACKINNON

Department of Geological Sciences, University of Canterbury, Christchurch, New Zealand

S. L. LONG

Department of Palaeontology, The Natural History Museum, Cromwell Road, London SW7 5BD

SYNOPSIS. Dall defined the Recent brachiopod genus *Laqueus* primarily on adult loop characteristics of the dorsal valve interior of a specimen in the US National Museum collection. However, he designated as the 'type species' *Terebratula californica* Koch in Küster, a taxon erected by Küster and based only on a single specimen consisting of conjoined valves exhibiting features of only the shell exterior. Küster's holotype is apparently lost; however, a restudy of available early figured material allegedly from California and attributed to *Terebratula californica* (more correctly, *T. californiana* Küster) by Dall, Sowerby and Davidson indicates a very high probability that Küster's holotype was misidentified by Dall. Further, Küster's holotype almost certainly did not originate from Californian waters, but more likely was collected from off Coquimbo, Chile, and is referable to, or closely allied to, *Magellania venosa* (Solander, 1789) which has a known geographic range extending from Coquimbo, Chile, to the Straits of Magellan and the Falkland Islands. Under Article 70.3 of the Rules of Nomenclature, we designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall. Specimens previously referred to *Laqueus californianus* (or *californicus*) from Californian waters are now referred to *Laqueus erythraeus* Dall, 1920. Specimens referred by other authors (listed in the Appendix) to *Laqueus californianus* (or *californicus*) occurring along the coasts of Washington, British Columbia and Alaska are now referred to *Laqueus vancouveriensis* Davidson, 1887.

INTRODUCTION

During the course of taxonomic reappraisals of diagnoses of brachiopod genera for the Treatise on Invertebrate Paleontology, Part H (currently under revision), an extensive literature search and investigation of available type and figured material of the genus *Laqueus* Dall, 1870, was undertaken. The investigation uncovered nomenclatural irregularities, including misinterpretation of the type species on which the genus *Laqueus* was founded, as well as frequent inconsistencies in the application of specific names to material collected along the Pacific coast of North America from California to Alaska (see Appendix). Given the longstanding importance of the genus in studies of Recent brachiopods we decided to undertake a critical review of the scientific literature that has dealt, over the past 130 years, with *Laqueus* species that occur in North American Pacific waters, with a view both to identifying and correcting past taxonomic irregularities and, equally importantly, promoting future stability of nomenclature of *Laqueus* species. We attribute much of the past confusion to the use by Dall (1870) of a specimen other than the holotype of the type species as the basis of his original generic diagnosis, and the failure of previous authors to establish the true identity and provenance of Dall's originally designated type species, *Terebratula californiana* Küster, 1844.

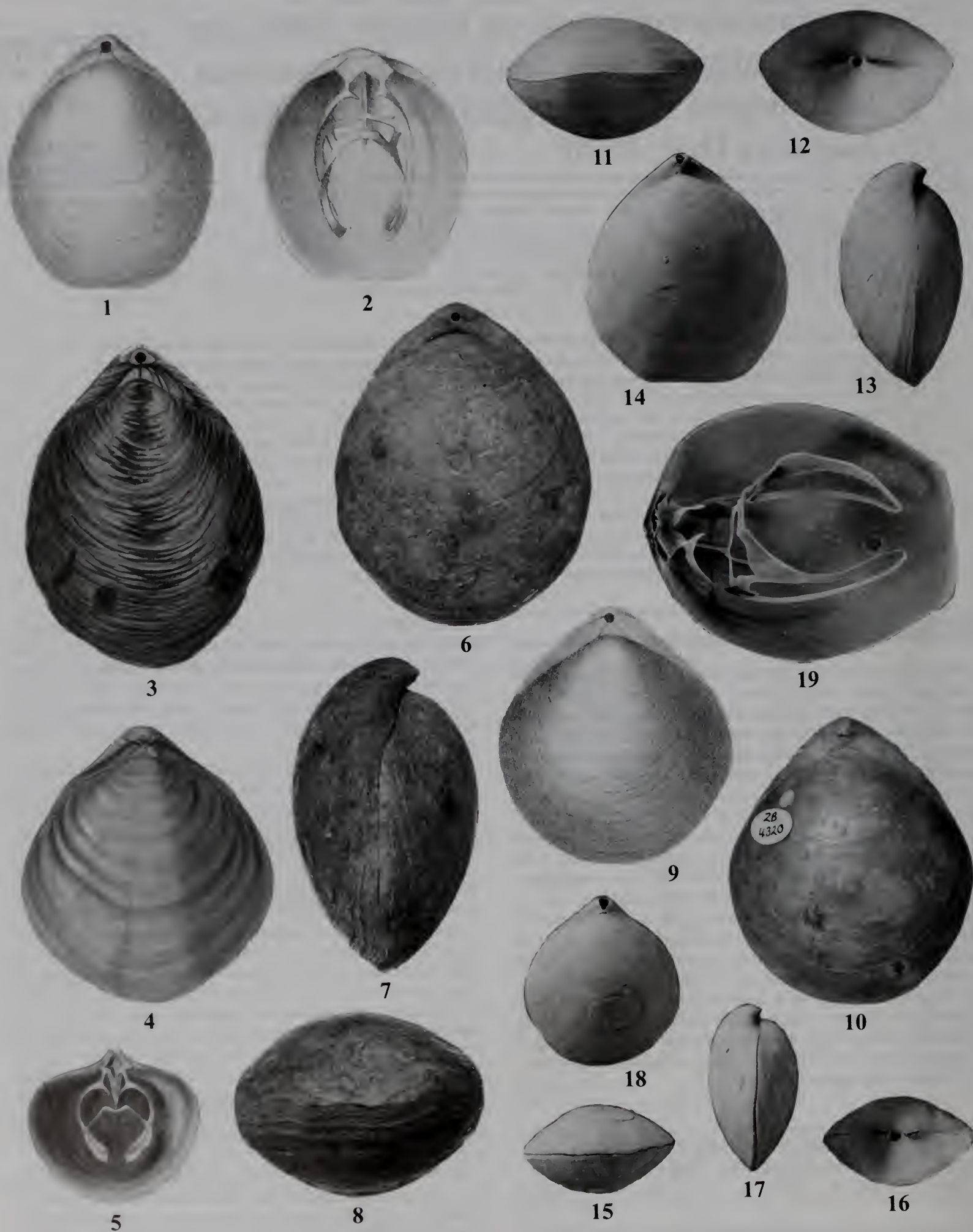
IDENTITY OF THE SPECIMEN USED IN THE ORIGINAL DIAGNOSIS OF THE GENUS *LAQUEUS* DALL, 1870

The name *Laqueus* was first established by Dall (1870) as a subgenus of *Terebratella* for brachiopods characterized by a distinctive form

of the adult loop in which 'the reflected part of the loop is attached by slender processes, one on each side, to the haemal processes (=descending branches in modern brachiopod loop terminology), not to the septum nor to the septal processes, at or near the points where the two septal processes (=lateral connecting bands in modern terminology) branch off to the septum'. Dall (1895) subsequently elevated the taxon to genus level.

Dall (1870) specified as 'Type' of his new subgenus *Laqueus*, *Terebratula californica* Koch (in Küster, 1844), but it is evident that his accompanying morphological description was based not on Küster's original figured specimen, but on a USNM specimen (Cat. No. 19395) collected from '80 fathoms, off Santa Catalina Island, California'. Dall (1870: pl. 7, fig. f) provided one illustration of a dorsal interior exhibiting the definitive adult *Laqueus* loop form, and an additional two relatively uninformative sketches (Dall, 1870: pl. 8, figs 9, 10) of the cardinalia and posterior shell exterior respectively. Superior illustrations of Dall's specimen (lent to Davidson by Dall), depicting a complete *Laqueus* loop, were also figured (as *Laqueus californicus*) by Davidson (1887: pl. 18, figs 7, 8, 8a). Two of Davidson's illustrations are reproduced herein as Figs 1, 2. Davidson's illustrations were subsequently reproduced in Oldroyd (1924) (as *Laqueus californicus*), in Thomson (1927) (as *Laqueus californicus*), and also in the Treatise on Invertebrate Paleontology, Part H, Brachiopoda (Hatai, 1965) (as *Laqueus californianus*). New photographic illustrations of the entire specimen, now minus loop, were figured by Hertlein & Grant (1944: pl. 21, figs 1–7) (as *Laqueus californianus*).

Some 50 years later, Dall (1920) provided another synonymy for *Laqueus californicus*, again citing '*Terebratula californica* Koch, in Chemnitz (*sic*)' as his original source, but in this later publication he removed the sole figured specimen of his 1870 publication (USNM Cat. No. 19395 – the specimen widely figured in later publications



on account of its distinctive loop) and designated that specimen the holotype of a new species *Laqueus erythraeus* Dall.

PROBABLE IDENTITY AND PROVENANCE OF THE HOLOTYPE OF *TEREBRATULA CALIFORNIANA* KÜSTER, 1844, ORIGINALLY DESIGNATED TYPE SPECIES OF THE GENUS *LAQUEUS* DALL

KÜSTER'S ORIGINAL TYPE SPECIMEN. Dall (1870) specified as 'Type' of his new subgenus *Laqueus*, '*Terebratula californica* Koch, Küster' 1844 (plate) 1848 (text). [Note: Dall's species name '*californica*' is a misspelling of Küster's original '*californiana*'; it is likely that Dall's misspelling (and the subsequent misspelling by various later authors) derives from an earlier misspelling by Sowerby (1846), followed by Carpenter (1864). Dall (and Carpenter) also followed Küster in incorrectly attributing the authorship of *T. californica* to Koch]. Küster inserted '*Terebratula californiana* Koch in litt.' immediately after his concise Latin diagnosis, but there is no record of Koch having ever formally published a description of the specimen described by Küster. Küster (1844: pl. 2b, figs 21–23) figured three views (dorsal, lateral and ventral) of the exterior of a single, large specimen with tightly conjoined valves but gave no interior views depicting the loop, or any other diagnostic internal characters. We refigure Küster's original illustration of the dorsal view as Fig. 3. Küster stated the locality as 'California' but gave no further details. The original description of *T. californiana* is somewhat unusual in that the species was named and illustrated by Küster in a part of his monumental revision of the 'Martini-Chemnitz Conchylien Cabinet' (second edition) that was published in 1844, whereas the description was not published until 1848.

Küster's holotype of *Terebratula californiana* could not be located by us and is presumed lost. However, his illustrations compare well with several specimens that were available to us in the brachiopod collections of The Natural History Museum, London, also attributed to the same species by near contemporaries of Küster, including Sowerby and Davidson, and placed in synonymy with *T. californiana* by Dall (1870 and 1920).

SOWERBY'S (1846) FIGURED SPECIMENS OF *TEREBRATULA CALIFORNICA*. In his synonymy of the type species of his new subgenus *Laqueus*, Dall (1870) listed a second reference to *Terebratula californica* Koch, that of Sowerby (1846) (the perpetrator of the original misspelling of *californiana* as *californica*), whose illustrations (Sowerby, 1846: pl. 70, figs 50–52) consisted of two exterior views and one dorsal interior with complete loop. Two of Sowerby's illustrations are refigured herein as Figs 4, 5. It must be stressed that the (teloform) loop structure depicted by Sowerby (op. cit.: pl. 70, fig. 52 and refigured herein as Fig. 5) for his *Terebratula californica* is quite dissimilar to that (bilateral) figured by Dall (1870: pl. 7, fig. f and refigured herein as Fig. 2) for allegedly the

same species (see Richardson, 1975, for explanations of brachiopod loop terminology, viz. teloform and bilateral). Sowerby's figured teloform loop is, however, comparable to that occurring in *Magellania venosa* (Solander, 1789). Indeed it is apparent that Dall (1920) subsequently recognized the discrepancy in the form of the Sowerby figured loop for, in his 1920 synonymy of *Laqueus californicus*, he again cited Sowerby (1847 (*sic*)), but this time included only Sowerby's two exterior views (plate 70, figs 50, 51) and specifically excluded Sowerby's interior with the teloform loop (plate 70, fig. 52) which he referred to *Magellania*.

DAVIDSON'S FIGURED SPECIMENS OF *LAQUEUS CALIFORNICUS*. Davidson (1887) was the first to take account of possible geographic variation in *L. californicus* by referring specimens collected from higher latitudes to a separate 'variety', *L. californicus* var. *vancouveriensis*, whilst retaining the binomen *L. californicus* for specimens hitherto known from Californian waters. It is our opinion that Davidson, in fact, presented illustrations of three distinct species, namely: (1) the Dall specimen (USNM 19395) from Santa Catalina Island, illustrating the *Laqueus* loop (Davidson, 1887: pl. 18, figs 7, 8, 8a); (2) two large specimens (including ZB 4417) attributable to Küster's species (Davidson, 1887: pl. 18, figs 6a–c, 9); (3) the specimens from higher latitudes attributed by Davidson to *L. californicus* var. *vancouveriensis* (Davidson, 1887: pl. 18, figs 10–13).

1. The Dall specimen (USNM 13395) (Figs 1, 2). This is the specimen which Dall (1920) subsequently designated as the holotype of *L. erythraeus*. We do not consider the specimen USNM 13395 to be conspecific with the Küster holotype. As the loop of Dall's diagnostic specimen is no longer preserved, Davidson's illustration of the loop (widely reproduced in later publications; Fig. 2) provides the best record of its appearance.
2. The specimens attributable to Küster's species. Davidson (1887: pl. 18, figs 6, 6a, 6b) figured three views of a large specimen (ZB 4417) with conjoined valves that bear very close resemblance in size, shape and appearance, to Küster's holotype of *Terebratula californiana*. Specimen ZB 4417 is well documented in The Natural History Museum's brachiopod collection as the specimen illustrated in Davidson (reproduced herein as Figs 6–8). There is no explicit documentation in The Natural History Museum's collections of the second specimen (Davidson, 1887: pl. 18, fig. 9; reproduced herein as Fig. 9) attributed to *Laqueus californicus* which, according to Davidson, is a reproduction of Küster's illustration (1844: pl. 2d, figs 1–3) of *Terebratula kochii* (Davidson's figure caption, p. 178, mistakenly quotes the Küster figure reference as 'tab. 2a, fig. 9' for this specimen).

Davidson's specimen (ZB 4417) with conjoined valves, still bearing original labelling, was examined by us and although the strong articulation of the valves precluded their total separation, it was possible to open the valves sufficiently to confirm that, despite the absence of a loop due to breakage, the internal morphology was unlike that attributable to any species of *Laqueus*.

Figs 1–19 Illustrations of specimens that have in the past been assigned to the genus *Laqueus* Dall. **1, 2**, Davidson's illustrations (Davidson 1887: pl. 18, figs 7, 8) of the USNM specimen 19395 assigned by him to *Laqueus californicus*, originally figured by Dall (1870), showing the distinctive *Laqueus* loop, × 1. **3**, Küster's original illustration of the holotype of *Terebratula californiana* (Küster 1844: pl. 2b, fig. 21), × 1. **4, 5**, Sowerby's illustrations (Sowerby 1846: pl. 70, figs 50, 52) of *Terebratula californica*, × 1. **6–8**, dorsal, lateral and anterior views of NHM specimen ZB 4417 assigned by Davidson (1887: pl. 18, figs 6, 6a, 6b) to *Laqueus californicus*, × 1. **9**, Davidson's illustration (Davidson 1887: pl. 18, fig. 9) of Küster's *Terebratula kochii*, assigned by Davidson to *L. californicus*, × 1. **10**, dorsal view of NHM specimen ZB 4320 of *Terebratula (Waldheimia) globosa* figured by Reeve (1860: pl. 2, species 3, fig. c), × 1. **11–14**, anterior, posterior, lateral and dorsal views of NHM specimen of *Laqueus erythraeus* Dall, ZB1001, × 1. **15–18**, anterior, posterior, lateral and dorsal views of NHM specimen of *Laqueus vancouveriensis* Davidson, ZB995, × 1. **19**, dorsal oblique view of dorsal interior of *Laqueus erythraeus* showing the loop, ZB4505, × 1.5.

We consider the internal morphology of this Davidson specimen (ZB 4417) suggests close affinity with *Magellania venosa* (Solander, 1789) which is unknown from Californian waters, and has a known range from Coquimbo, Chile, to the Straits of Magellan and the Falkland Islands. We also consider that the second specimen referred by Davidson to *L. californicus* (Davidson, 1887: pl. 18, fig. 9) should be referred to the genus *Magellania* (aff. *M. venosa*). Indeed the Davidson specimen (ZB 4417) bears strong resemblance both internally and externally to the '*Terebratula* (*Waldheimia*) *globosa*' figured by Reeve (1860: pl. 2, species 3, fig. c), and refigured by us as Fig. 9, which was synonymised by Davidson (1887: 112) with *Laqueus californicus*. The loop of Reeve's specimen (ZB 4320), though only partially intact, is unmistakably teloform (as in *M. venosa* but not *Laqueus*) and is almost certainly conspecific with the Davidson specimen (ZB 4417). Furthermore, Reeve quotes two localities viz. 'California, Coquimbo'. We are strongly of the opinion that the 'California' location attributed to Davidson's, Reeves', Sowerby's and Küster's specimens of *L. californicus* is erroneous and that Coquimbo (Chile) is a more likely source. The strong similarity of Davidson's, Reeves', and Sowerby's specimens of *L. californicus* (and the inferred similarity of the Küster holotype) to *Magellania venosa* is apparent but further investigation of the material is required, especially with regard to provenance.

3. The Vancouver Island specimens. According to Davidson (1887), Dall (personal communication, 1884) referred brachiopod assemblages from the vicinity of Vancouver Island, British Columbia, Canada, to *L. californicus*. Davidson considered the morphology of the Vancouver Island assemblages to be sufficiently different (smaller size, comparatively larger pedicle foramen) from his (undifferentiated) Californian assemblages to merit recognition as a distinct variety, namely *L. californicus* var. *vancouveriensis* and he illustrated them as such (Davidson, 1887: pl. 18, figs 10–13b). Adult specimens of Davidson's *L. californicus* var. *vancouveriensis* possess a typical *Laqueus* (bilateral) loop and are not considered by us to be conspecific with the Küster holotype.

LAQUEUS JEFFREYSI DALL, 1895. In his initial study, Dall (1870) erected only two species of *Laqueus*, namely *L. californicus* from Californian waters, and *L. suffusus* from Japan. Following examination of extensive collections (listed in Dall 1920: 348–349) made by the U.S. Fish Commission steamer Albatross from the Aleutian Islands to California, Dall (1895: 725) referred specimens of the Davidson variety *vancouveriensis* to a new species *L. jeffreysi*, and it is clear from Dall's discussion that he was applying the name *jeffreysi* to what he referred to informally as 'the northern form', whilst retaining the species name *californicus* for 'the southern form' occurring off Santa Catalina Island.

There is, however, confusion over the validity of the name *jeffreysi* for that species, as *jeffreysii* (*sic*) had been used previously by Dall in three separate publications (firstly as *Frenula jeffreysii* (*sic*) (Dall, 1871a: 55); secondly as *Ismenia? jeffreysi* (Dall, 1871b: 65); thirdly as *Megerlia* (*Ismenia*) *jeffreysi* (Dall, 1873: 187)) for small brachiopods presented to him by J. Gwyn Jeffreys that had been recovered from northeast Atlantic waters. In a fourth publication, Dall (1877) united the abovementioned northeast Atlantic specimens with additional brachiopods from the northeast Pacific, collected by Dall from the Semidi Islands and Port Etches and by J. Richardson from Vancouver Island, Victoria, British Columbia, all under the name *Megerlia jeffreysi*. Having erected the genus *Laqueus* in 1870, prior to the publication of his reports on those specimens to which he applied the species name *jeffreysi*, it is evident that Dall, at that time

(1877), did not consider any of his Northeast Pacific specimens to be referable to *Laqueus*. In his 1895 publication, however, it is evident that Dall had changed his mind, now referring *all* his previous *jeffreysi* specimens to the genus *Laqueus*. Subsequently, having by that time realized that the Northeast Atlantic specimens to which he originally applied the species name *jeffreysi* were, in fact, juveniles of *Macandrevia cranium* (Müller), Dall (1920) abandoned the use of *jeffreysi* and reverted to employing Davidson's 'variety', *Laqueus californicus vancouveriensis* for the U.S. National Museum's approximately 185 specimens of his 'northern form', occurring from 'South East Alaska Peninsula' to the 'Washington coast'. As well as listing the many specimens attributable to *Laqueus californicus vancouveriensis*, Dall (1920) also listed some forty specimens under the heading '*L. californicus*, typical', mainly from Californian waters, but the list excluded his specimens of the large reddish-tinted form from off Santa Catalina Island, which include specimen USNM 19395, for which Dall (1920) established his new species *Laqueus erythraeus*.

LAQUEUS ERYTHRAEUS DALL, 1920. Dall (1920) did not provide an accompanying morphological description of his new species, but it is obvious that since his original description of *L. californicus* (Dall, 1870) was based on specimen USNM Cat. No. 19395 from Santa Catalina Island, his 1870 description now (in 1920) applied to *L. erythraeus*. Whilst not explicitly saying so, Dall appeared to separate *L. erythraeus* from *L. californicus* (*sic*) on the basis of size, shape, colour, and possibly also biogeographic extent. The etymology of the species name *erythraeus* (from the Greek *erythros*, red) is a clear reference to the strong reddish shell coloration so typical of Californian specimens of *Laqueus*. Although it is clear that the holotype of *Laqueus erythraeus* is USNM 19395, Dall (1920) also included in his synonymy two references by Carpenter (1864). However, page citations in Carpenter (1864) contain no new descriptions or illustrations but are merely taxonomic listings of earlier authors. Carpenter's citation on page 568 refers to specimens of '*Terebratula* (*Waldheimia*) *globosa* (Val), Lam.' figured in Reeve's 'Conchologia Iconica; Terebratulidae' (Reeve, 1860) which he (Carpenter) synonymises with '*T. californica* Koch'. Carpenter's citation on page 574 refers to an entry in an earlier publication (Trochel's 'Archives für Natur') which reads '1849. Vol. II, p. 99 *Terebratula Californica*, Linsley'. Also listed in Dall's synonymy (Dall, 1920), was an additional Carpenter (1864) reference – '*Waldheimia californica* CARPENTER, Supple. Rep. Brit. Assoc., p. 636, 1864' – but this entry is part of a table of localities with no illustration or description given. Dall's references to Carpenter's earlier citations are thus erroneous and further confuse rather than assist any understanding of the new species, *L. erythraeus*.

Specimen USNM 19395 was subsequently figured by Hertlein & Grant (1944) as '*Laqueus californianus* Koch. Type of *Laqueus erythraeus* Dall'. Hertlein & Grant (1944: pl. 21, figs 1–7) figured five exterior and two interior views of specimen USNM 19395: the dorsal interior (previously figured by Dall and Davidson) no longer has the loop preserved. Hertlein & Grant (1944) rejected Dall's taxonomic revision, synonymising *L. erythraeus* once again with *L. californianus* and adding the statement (p. 146), '*Laqueus erythraeus* Dall appears to be an individual variation and not entitled to taxonomic recognition'. Hertlein & Grant were clearly unaware of any discrepancy in the identity of the originally designated holotype of *L. californianus*, viz. *Terebratula californiana* Küster, 1848 and on the basis of the evidence presented herein regarding the longstanding lack of awareness of the misidentified Küster type, we resurrect the species *L. erythraeus* (holotype USNM 19395) as a valid species and, under Article 70.3 of the Rules of Nomenclature (ICZN, 1999),

we herein designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall, 1870.

LAQUEUS VANCOUVERIENSIS DAVIDSON, 1887. Davidson's *Laqueus californicus* var. *vancouveriensis* (Dall's 'northern form') was elevated to full species rank by Hertlein & Grant (1944) who provided a comprehensive synonymy and extensive biogeographic and stratigraphic records of the species. It is obvious that Hertlein & Grant applied the species name *vancouveriensis* to all material collected along the North American Pacific coast north of California, and were doubtful of earlier records of the species from Californian waters. We agree with Hertlein & Grant's differentiation of *vancouveriensis* as a full species. We are aware that various authors from the mid-1960's to the present have applied the name *Laqueus californianus* (or *californicus*) to specimens collected from waters off British Columbia and Washington (see Appendix). In line with Hertlein & Grant (1944) we believe that those specimens are more correctly referable to *Laqueus vancouveriensis* and we advocate that all future collections from north of California (exhibiting typical *L. vancouveriensis* morphology as described by Hertlein & Grant) be identified as such.

CONCLUSIONS

1. Küster's original holotype of *Terebratula californiana* was misidentified by Dall (1870). The holotype of *T. californiana* and various other specimens referred by nineteenth century workers to the species show strong affinity with *Magellania venosa* and were probably collected from waters off Coquimbo, Chile, not California. Consequently, use of the species name *californianus* (or *californicus*), as previously applied to North American *Laqueus* assemblages, should be abandoned.
2. Under Article 70.3 of the ICZN (1999), we herein designate *Laqueus erythraeus* Dall, 1920, as the type species of the genus *Laqueus* Dall, 1870.
3. Specimens previously referred to *Laqueus californianus* (or *californicus*) from Californian waters should now be referred to *Laqueus erythraeus* Dall, 1920.
4. Specimens previously referred to *Laqueus californianus* (or *californicus*) occurring along the coasts of Washington, British Columbia and Alaska should now be referred to *Laqueus vancouveriensis* Davidson, 1887.

ACKNOWLEDGEMENTS. D.I.M. gratefully acknowledges the provision of study leave by the University of Canterbury, New Zealand and the provision of working facilities in the Department of Palaeontology at The Natural History Museum, London, where this work was carried out. The Photographic Unit of The Natural History Museum is thanked for photographing specimens and plates. We thank C.H.C. Brunton for reading an earlier draft of our manuscript.

REFERENCES

Alexander, R. R. 1990. Mechanical strength of shells of selected extant articulate brachiopods; implications for Paleozoic morphologic trends. *Historical Biology*, 3: 169–188.

Bernard, F. R. 1972. The living Brachiopoda of British Columbia. *Syesis*, 5: 73–82.

Carpenter, P. P. 1864. Supplementary report on the present state of our knowledge with regard to the Mollusca of the West Coast of North America. *Report of the 33rd Meeting of the British Association for the Advancement of Science; held at Newcastle-upon-Tyne in August and September 1863*: 517–686. John Murray, London.

Cohen, B. L. & Gawthrop, A. B. 1997. The brachiopod genome. In: Kaesler, R. L. (ed.)

Treatise on Invertebrate Paleontology. Part H, Revised. Brachiopoda (Introduction): 189–212. University of Kansas & Geological Society of America. Lawrence.

—, — & Cavalier-Smith, T. 1998. Molecular phylogeny of brachiopods and phoronids based on nuclear-encoded small subunit ribosomal RNA gene sequences. *Philosophical Transactions of the Royal Society, London, Series B*, 353: 2039–2061.

Collins, M. J., Curry, G. B., Quinn, R., Muyzer, G., Zomerdruk, T. & Westbroek, P. 1988. Sero-taxonomy of skeletal macromolecules in living terebratulid brachiopods. *Historical Biology*, 1: 207–224.

Dall, W. H. 1870. A revision of the Terebratulidae and Lingulidae, with remarks on and descriptions of some Recent forms. *American Journal of Conchology*, 6: 88–168.

— 1871a. A new genus of brachiopods (sic). *American Naturalist*, 5: 55.

— 1871b. Supplement to the 'Revision of the Terebratulidae,' with additions, corrections and a revision of the Craniidae and Discinidae. *American Journal of Conchology*, 7: 39–85.

— 1873. Catalogue of the Recent species of the Class Brachiopoda. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1873: 177–204.

— 1877. Report on the Brachiopoda of Alaska and the adjacent shores of Northwest America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 1877: 155–170.

— 1895. Scientific results of explorations by the U. S. Fish Commission Steamer Albatross. No. 34 – Report of Mollusca and Brachiopoda dredged in deep water, chiefly near the Hawaiian Islands, with illustrations of hitherto unfigured specimens from North America. *Proceedings of the U. S. National Museum*, 17: 615–733.

— 1920. Annotated list of the Recent Brachiopoda in the collection of the United States National Museum, with descriptions of thirty-three new forms. *Proceedings of the U. S. National Museum*, 57: 261–377.

Davidson, T. 1887. A Monograph of Recent Brachiopoda. Part II. *Transactions of the Linnaean Society of London, 2nd Series, Zoology*, 4: 75–182.

Emig, C. C. 1992. Functional disposition of the lophophore in living Brachiopoda. *Lethaia*, 25: 291–302.

Fraser, C. M. 1932. A comparison of the marine fauna of the Nanaimo Region with that of the San Juan Archipelago. *Royal Society of Canada, Transactions, Series 3, Section 4*, 26: 49–70.

Hatai, K. M. 1938. On some Cenozoic Brachiopoda from the North American region. *American Midland Naturalist*, 19: 706–722.

— 1965. Family Laqueidae. In: Moore R. C. (ed.) *Treatise on Invertebrate Paleontology. Part H: Brachiopoda*: 845–846. University of Kansas Press, Geological Society of America, Lawrence.

Hertlein, L. G. & Grant, U. S. 1944. The Cenozoic Brachiopoda of Western North America. *Publications of the University of California at Los Angeles in Mathematical and Physical Sciences*, 3: 1–236.

— & — 1960. The geology and paleontology of the marine Pliocene of San Diego, California. *Memoirs of the San Diego Society for Natural History*, 2: 73–133.

ICZN. 1999. *International code of zoological nomenclature*. Fourth Edition. International Trust for Zoological Nomenclature, London. xxix + 306 pp.

Konzhukova, E. D. 1957. Plechenogie (Brachiopoda) dal'nevostochnykh morei. (Brachiopoda of the Far Eastern Seas of the USSR.). *Issledovaniia Dal'nevostochnykh Morei SSSR*, 4: 5–84.

Küster, H. C. 1843–48. Mollusca, Brachiopoda. Terebratulacea. Lochsmuscheln. In: Martini-Chemnitz Conchylien Cabinet, second edition, 7: pls 2, 2b, 2c, 2d, 3, 4 (1844), pp. 25–49 (1848). [The plates and plate descriptions of *Terebratula californiana* were published separately in 1844 prior to the publication of the text in 1848]

LaBarbera, M. C. 1977. Brachiopod orientation to water movement. 1. Theory, laboratory behaviour and field orientations. *Paleobiology*, 3: 270–287.

— 1981. Water flow patterns in and around three species of articulate brachiopods. *Journal of Experimental Marine Biology and Ecology*, 55: 185–206.

— 1986. Brachiopod lophophores: functional diversity and scaling. In: Racheboeuf, P. R. & Emig, C. C. (editors), *Les Brachiopodes Fossiles et Actuels. Biostratigraphie du Paléozoïque*, pp. 313–321. Lyon.

Lowenstam, H. A. 1961. Mineralogy, O¹⁸/O¹⁶ ratios, and strontium and magnesium contents of recent and fossil brachiopods and their bearing on the history of the oceans. *Journal of Geology*, 69: 241–260.

Nomura, S. & Hatai, N. M. 1937. A list of the Northwest American Cenozoic Brachiopoda contained in the Division of Geology of the Saito Ho-On Kai Museum, compared with similar forms of the Japanese Northeast Cenozoic. *Saito Ho-On Kai Museum of Natural History, Research Bulletin*, 13: 179–188.

Oldroyd, I. S. 1924. The marine shells of the West Coast of North America. *Stanford University, Publications, Geological Sciences*, 1: 221–232.

Reeve, L. A. 1860. *Conchologica Iconica; or, illustrations of the shells of molluscos animals; volume XIII, monograph of the genus Terebratula*. L. Reeve and Co., London. 8 pp, pls 2–5.

Reynolds, W. A. & McCammon, H. M. 1977. Aspects of the functional morphology of the lophophore in articulate brachiopods. *American Zoologist*, 17: 121–132.

Richardson, J. R. 1975. Loop development and the classification of terebratellacean brachiopods. *Palaeontology*, 18: 285–314.

Sass, D. B., & Monroe, E. A. 1967. Shell-growth in Recent terebratuloid Brachiopoda. *Palaeontology*, 10: 298–306.

- Semenov, V. N. 1965. (The quantitative distribution of the bottom fauna on the shelf and the upper continental slope in the Gulf of Alaska.). *Vsesoiuznyi Nauchno-Issledovatel'skii Institut Morskogo Rybnogo Khoziaistva i Okeanografii (VNIRO), Trudy*, 58: 49–78.
- Smith, A. G. & Gordon, M. Jr. 1948. The marine mollusks and brachiopods of Monterey Bay, California, and Vicinity. *California Academy of Sciences, Proceedings, Series 4*, 26: 147–245.
- Solander, D. C. 1789. *Anomia venosa*. In: Dixon, G. A *Voyage Round the World; but more particularly to the northwest coast of America: performed in 1785-88, in the King George and Queen Charlotte, Captains Portlock and Dixon &c*, p. 355, pl. 11. London.
- Sowerby, G. B. 1846. *The Recent Brachiopoda: Thesaurus Conchyliorum, or Monographs of genera of shells*, 1: 337–371. Sowerby, London.
- Staisny, G. 1933. Verzeichnis der Brachiopoden-Sammlung des Naturhistorischen Reichsmuseums in Leiden. *Zoologische Mededelingen*, 15: 129–148.
- Strathmann, R. R. 1973. Function of lateral cilia in suspension feeding of lophophorates (Brachiopoda, Phoronida, Ectoprocta). *Marine Biology*, 23: 129–136.
- Thayer, C. W. 1975. Size-frequency and population structure of brachiopods. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 17: 139–148.
- 1986a. Are brachiopods better than bivalves? Mechanisms of turbidity tolerance and their interaction with feeding in articulates. *Paleobiology*, 12: 161–174.
- 1986b. Respiration and the function of brachiopod punctae. *Lethaia*, 19: 23–31.
- Thomson, J. A. 1927. Brachiopod morphology and genera (Recent and Tertiary). *New Zealand Board of Science and Art, Manual*, 7: 138 pp.
- Tunncliffe, V. J. & Wilson, K. 1988. Brachiopod populations – distribution in fjords of British Columbia and tolerance of low Oxygen concentrations. *Marine Ecology-Progress Series*, 47: 117–128.
- Weaver, C. E. 1942. Paleontology of the marine Tertiary formations of Oregon and Washington. *University of Washington, Publications in Geology*, 5: 1–274.
- Woodring, W. P., Bramlette, M. N. & Kew, W. S. W. 1946. Geology and Paleontology of Palos Verdes Hills, California. *U.S. Geological Survey Professional Paper*, 207: 145 pp.

APPENDIX

Representative list of citations of northeast Pacific *Laqueus* species names (variously spelled) and localities referred to in the literature since 1924.

Laqueus californicus

- | | |
|---------------------|---|
| Oldroyd 1924 | British Columbia to off Point Loma, California. |
| Thomson 1927 | British Columbia to California (Recent); California (Pliocene). |
| Fraser 1932 | Nanaimo Region, Vancouver Island, British Columbia. |
| Staisny 1933 | Santa Catalina, California. |
| Nomura & Hatai 1937 | Off San Pedro, California. |
| Hatai 1938 | British Columbia to California (Recent); California (Pliocene). |

- Lowenstam 1961
- Semenov 1965
- Sass & Monroe 1967
- Reynolds & McCammon 1977
- Collins *et al.* 1988
- Emig 1992

Laqueus californianus

- Smith & Gordon 1948
- Hertlein & Grant 1944
- Hertlein & Grant 1960

- Bernard 1972

- Strathmann 1973
- Thayer 1975, 1986
- LaBarbera 1977, 1981, 1986

- Tunncliffe & Wilson 1988
- Alexander 1990
- Cohen & Gawthrop 1997
- Cohen *et al.* 1998

Laqueus californicus convexus

- Konzhukova 1957

Laqueus californicus vancouverensis

- Oldroyd 1924

- Thomson 1927

Laqueus vancouverensis

- Hatai 1938

- Hertlein & Grant 1944

Laqueus aff. vancouverensis

- Weaver 1942

Laqueus vancouveriensis

- Hertlein & Grant 1960
- Thayer 1986

Laqueus vancouveriensis diegensis

- Hertlein & Grant 1960

Laqueus erythraeus

- Oldroyd 1924
- Thomson 1927

Laqueus jeffreysi

- Woodring *et al.* 1946

- Santa Catalina, California.
- Gulf of Alaska.
- Santa Catalina, California.
- San Juan Island, Washington.
- Friday Harbour, Washington.
- San Juan Island, Washington.

- Point Pinos, Monterey Bay, California.
- California.

- British Columbia to Point Loma, California; S. California (Middle Pliocene).

- Queen Charlotte Island, British Columbia to California and also the Sea of Japan.

- San Juan Island, Washington.

- San Juan Island, Washington.

- San Juan Island, Washington; Iceberg Point, Washington.

- British Columbia.

- Puget Sound.

- Bamfield, British Columbia.

- Bamfield, British Columbia.

- Tatar Strait, northern Sea of Japan.

- Southeast Alaska. Kodiak Island, Juneau Harbour, Forrester Island; off British Columbia; Juan de Fuca Strait, Puget Sound, Washington coast.

- S.E. Alaska to Washington; California (Pliocene).

- S.E. Alaska Peninsula to Washington; California (Pliocene).

- British Columbia.

- Olympic Peninsula, Washington to Queen Charlotte Island, British Columbia (Upper Eocene).

- Aleutian Island to Puget Sound.
- Iceberg Point, Washington.

- South California, Lower California, Mexico (Middle Pliocene).

- Catalina Island, California.

- Catalina Island, California.

- San Pedro, California (Pleistocene).